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G. E. Rehfeldt

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RESEARCH SUMMARY

Fall frost injury to 159 seedlots of 2-year-old Douglas-fir seedlings growing at a nursery in Coeur d'Alene, ID, provided an opportunity to verify experimental models that describe genetic variation in freezing tolerance to populations from the Inland Northwest. Experimental results of three previous studies were updated and then were combined to provide a single model of freezing tolerance. According to the model, elevation and geographic location of the seed source accounted for 67 percent of the variance in freezing injury to 167 populations. Injury predicted by this model to nursery-grown seedlots was significantly correlated (r = 0.67) with the injury observed in the field.

THE AUTHOR

G. E. REHFELDT is a plant geneticist at the Intermountain Research Station's Forestry Sciences Laboratory in Moscow, ID. He has been studying the ecological and quantitative genetics of Rocky Mountain conifers since 1968.

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Intermountain Research Station
324 25th Street
Ogden, UT 84401

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INTRODUCTION

In the Inland Northwest, Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) occupies a broad range of environments that vary in frost-free period from 60 to 150 days (USDA Forest Service 1965). Populations, however, are physiologically attuned to only a segment of this environmental gradient (Rehfeldt 1984). When acclimating in a common environment, populations within northern Idaho (Rehfeldt 1979a, 1979b), western Montana (Rehfeldt 1982), and central Idaho (Rehfeldt 1983) display a differential tolerance to early fall frosts. Mathematical models developed for each of these three geographic regions have related genetic variation to the elevation and geographic location of the seed source. These models have generally shown that populations from areas characterized by short growing seasons suffer less injury from fall freezing than do populations from mild environments.

An opportunity to verify models was provided by fall frost injury to 2-year-old Douglas-fir seedlings growing at the USDA Forest Service nursery at Coeur d'Alene, ID. This opportunity also provided the stimulus for (1) updating all three models by using recent procedures for constructing adaptive landscapes and (2) developing a single model to describe genetic variation within the Inland Northwest.

MATERIALS AND METHODS

Three studies (table 1) of tolerance to fall freezing assessed differentiation of Rocky Mountain populations in common gardens but under much different experimental conditions. All studies involved a different set of populations acclimating in different years. In one study tolerance was assessed throughout acclimation, but in the other two tolerance was observed on a single date. In one, a natural frost induced differential injury to seedlings in a field test; in the other two, a laboratory chamber was used to freeze detached twigs. Injury from the natural freeze occurred on a single night and represents a single treatment that induced a mean injury of only 8 percent; that in the laboratory resulted from numerous treatments that produced a range in mean injury from nearly zero to almost 100 percent. As a result, the freezing tolerance exhibited by a population in a given study was not directly comparable to the tolerance of populations in other studies.

Consequently, the development of a model describing genetic variation in freezing tolerance for the entire region required, first, a single data set normally distributed about a common mean and, second, a data set within which the ranking of populations accurately depicted genetic variation uninfluenced by the different testing procedures. While the former condition was

Table 1—Summary of studies of freezing tolerance to Douglas-fir populations

Characteristic	Study 1[1]	Study 2[2]	Study 3[3]
Geographic region	Northern Idaho	Western Montana	Central Idaho
Number of populations	43	56	73
Origin of freeze	Laboratory	Laboratory	Nature
Time of freeze	Sept. to Nov.	mid-September	mid-September
Mean injury (pct)	49	39	8
Binomial variance	0.0058	0.0042	0.0010
Experimental model			
Independent variables	7	6	16
R^2	0.38	0.35	0.48

[1] Rehfeldt 1979b.
[2] Rehfeldt 1982.
[3] Rehfeldt 1983.

solved with transformations, the latter was met by scaling data sets according to the differential performance of populations common among studies.

As a first step, the effect of differential mean injury for the studies was eliminated by defining a deviation:

$$P'_{ij} = (P_{ij} - \bar{P}_j) + 0.5$$

where P_{ij} is the proportion of injured seedlings from population i in study j, and $\bar{P}_j$ is the mean for study j. The constant was added to ensure that $P' > 0$ and to provide deviates about a mean value of 50 percent.

Next, normality was obtained by means of the logistic transformation suited for binomial data (Finney 1971). A logit, Y_{ij}, was weighted according to the variance in each study:

$$Y_{ij} = \ln[(1 - P'_{ij})/P'_{ij}]/[(\bar{P}_j)(1 - \bar{P}_j)n_j^{-1}]$$

where n_j is the number of populations in study j.

Finally, all data were scaled to those from northern Idaho according to the differential performance of populations common among studies. Thus, Y'_i was defined such that:

1. If $j = 1$, $Y'_i = Y_{i1}$
2. If $j = 2$, $Y'_i = Y_{i2} + SF_1$
3. If $j = 3$, $Y'_i = Y_{i3} + SF_2$

where the scaling factor, SF_1, is the average difference between test 1 and test 2 performance of two populations common to studies 1 and 2 and SF_2 is the average difference between test 1 and test 3 performance of three populations common to studies 1 and 3.

These procedures produced a single data set of freezing injury to 167 populations that was normally distributed about a common mean. To combine data sets in this manner, however, does not allow the effectiveness of the procedures to be tested statistically. Effectiveness can only be interpreted according to the degree by which the combined model (1) coordinates the individual models and (2) is biologically plausible.

The combined model of genetic variation in freezing tolerance was developed from a stepwise regression program for maximizing R^2 (SAS 1979). The program used elevation, latitude, longitude, northwest departure, and southwest departure plus their squares as independent variables. The northwest and southwest departures were obtained by rotating the grid of latitude and longitude by 45°. Geographic variables were nested within regions to allow a given independent variable an opportunity to describe contrasting patterns of variation in different geographic regions. Consequently, 26 independent variables were available for stepwise regression of the general form:

$$Y'_i = \beta_0 + \beta_1 E_i + \beta_2 E_i^2 + \sum_{j,k} \gamma_{jk} X_{ijk} + \sum_{j,k} \delta_{jk} X_{ijk}^2$$

where

E_i is the elevation of population i

X_{ijk} is geographic variable k for population i in region j

β_0, β_1, β_2, γ_{jk}, and δ_{jk} are regression coefficients

$k = 1 \ldots 4$

$j = 1 \ldots 3$.

Adequacy of the stepwise model was determined by the level of significance, the size of the residual mean square, and a lack of patterning displayed by the residuals (Draper and Smith 1981). The model meeting these criteria was used to predict frost injury to the seedlots represented in nursery production beds.

Frost injury to 2-year-old seedlings growing at the Coeur d'Alene Nursery occurred on September 28, 1984, when temperatures reached −3 °C after a prolonged period of warm weather. Differing injury occurred to 179 seedlots, which comprised the 5 million 2-year-old Douglas-fir seedlings being grown. Of these seedlots, 159 were from the regions represented by the experimental model.

In late October, four plots of 100 seedlings were established at equidistant intervals within each seedlot, regardless of size. The sample thus comprised about 1.5 percent of the planted trees. Injury was scored according to browning of leaves and was recorded as a proportion of injured trees for each seedlot. After the logit transformation, these binomial data were then correlated with those predicted by the model that had been developed from experimental data.

RESULTS AND DISCUSSION

The best fitting stepwise regression model included 16 variables and accounted for 67 percent of the variance in freezing tolerance of populations. The model describes geographic clines for a common elevation (fig. 1) and elevational clines for various geographic localities (fig. 2). Percentage scales in these figures were converted from the weighted logit transformation by using a variance among populations that was pooled for the three studies.

Geographic patterns portrayed by the model for a constant elevation indicate that populations from north-central Idaho exhibit the most injury (smallest logits). In fact, mean values for populations from this area deviate from the mean by more than two standard deviations (about 18 percent injury). From this area, freezing tolerance of populations increases in all directions, but clines are particularly steep across the rugged Bitterroot Range to the west and across the Salmon Drainage to the south.

Geographic clines at a constant elevation follow geographic patterns of frost-free period (U.S. Department of Commerce 1968) even though geographic trends in frost-free period are not independent of elevation. Thus, the populations from north-central Idaho that exhibit highest freezing injury (lowest weighted logit) come from an area typically having long frost-free periods (120 to 150 days at 800 m elevation). And, corresponding to the genetic patterns of figure 1, the average frost-free season gradually declines to the north (90 days at 900 m) and rapidly drops to less than 60 days in the rugged mountains to the east and southeast.

The elevational clines (fig. 2) are presented for localities on three of the geographic isopleths (fig. 1). Like the geographic clines, elevational clines (fig. 2) closely parallel the declining frost-free period associated with increasing elevation. According to Baker (1944), the frost-free period changes by about 90 days across an elevational interval of 1,000 m. In association, regression models predict that populations from 800 and 1,800 m at the

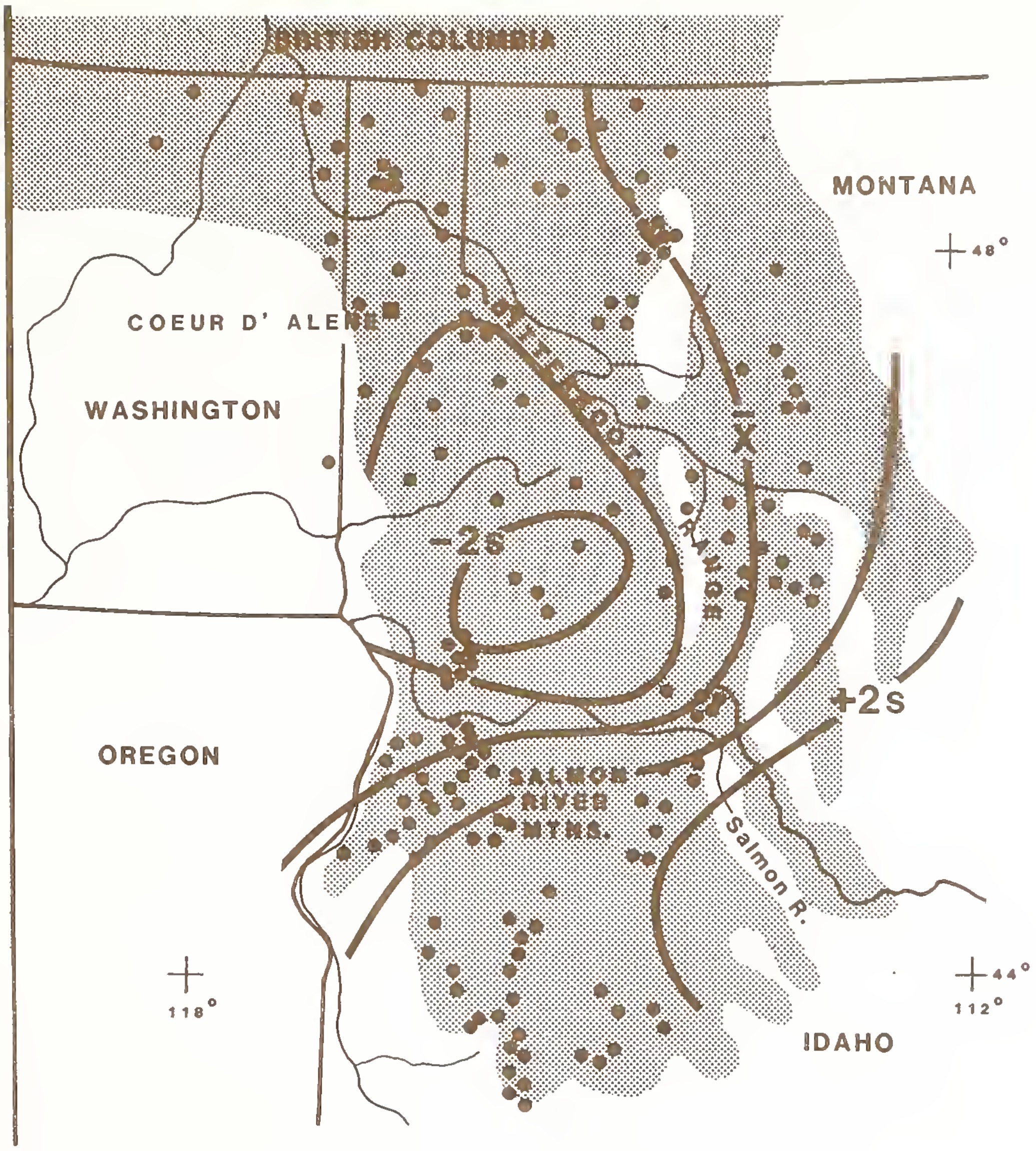

Figure 1—Geographic patterns of genetic variation presented as isopleths of equal performance for the mean elevation (1,420 m). Isopleths are arranged relative to the mean predicted injury (x̄) with an interval between isopleths equal to the standard deviation which corresponds to approximately 9 percent injury. Shading represents the distribution of Douglas-fir, and dots locate populations represented in the experimental data.

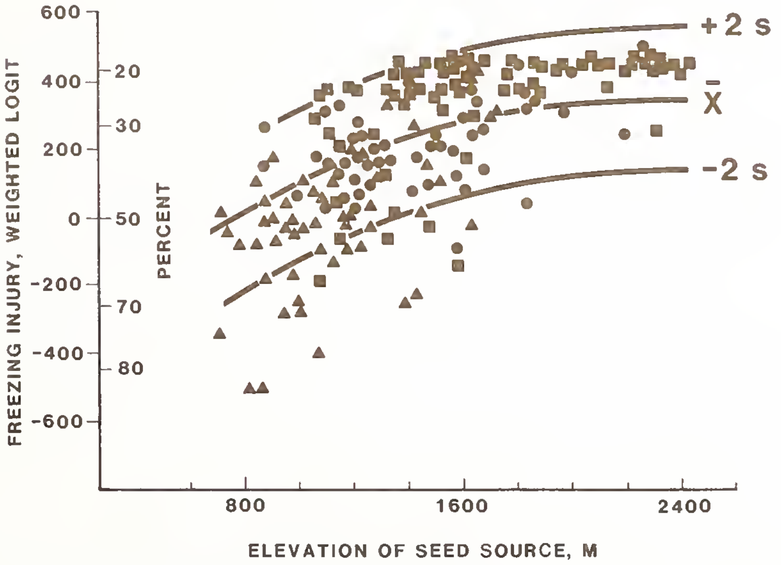

Figure 2—Elevational clines of freezing injury for localities along three geographic isopleths (figure 1). ▲ = northern Idaho, ● = western Montana, ■ = central Idaho.

same geographic locality will differ in freezing injury by about 25 percent when mean injury is 50 percent. The model also describes a nonlinear cline that was undoubtedly accentuated by a lack of injury to most central Idaho populations from above 1,600 m. The nonlinear trend, however, was also apparent in studies for western Montana (fig. 2) and, therefore, is not completely attributable to the low mean injury associated with study 3. Apparently elevations above 1,800 m are of relatively uniform severity, and additional adaptive differentiation fails to occur in Douglas-fir.

By describing genetic variation in relation to environmental gradients, the model could be used to predict relative frost injury to the seedlots growing in the production nursery at Coeur d'Alene. The relationship between predicted injury and observed injury was not only statistically significant (1 percent level) but also accounted for 45 percent (r = 0.67) of the variance in observed injury (fig. 3). There is no doubt, therefore, that the model was effective in predicting actual injury. Effectiveness, moreover, is not compromised by the scatter about regression (fig. 3). Relatively large residuals should be expected when the injury observed at Coeur d'Alene involved (1) a low mean injury (7 percent), (2) trees spread across 8.5 acres of production beds, and (3) a nonreplicated, systematic planting in which seedlots from the same National Forest were in adjacent beds.

Results support three general conclusions. First, the observed injury at Coeur d'Alene validates the model of genetic variation developed from experimental data. Second, artificial freezing of detached twigs mirrors the relative amounts of damage expected for intact plants subjected to natural freezing. And finally, relatively steep elevational and geographic clines describe genetic variation in freezing tolerance of Douglas-fir populations in the Rocky Mountains.

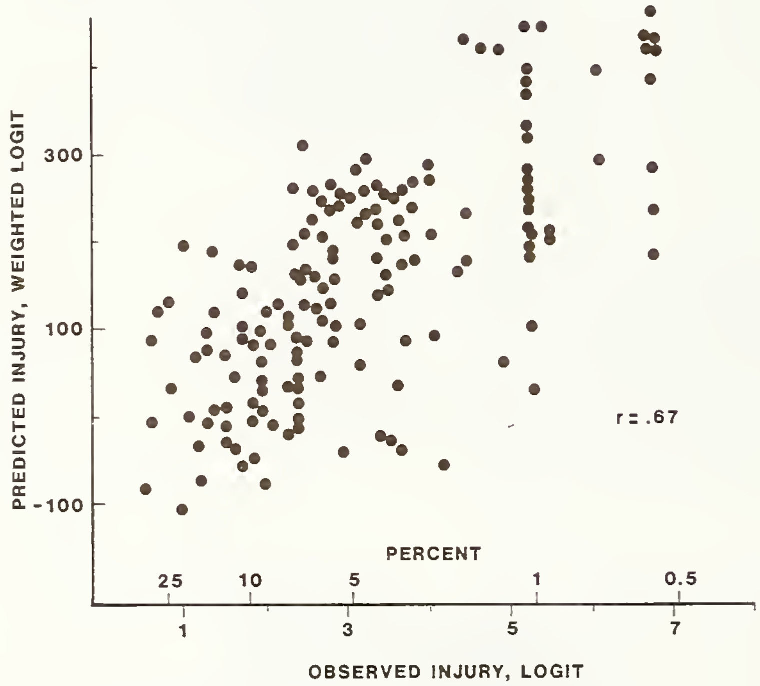

Figure 3—Relationship between observed frost damage to seedlots at the Coeur d'Alene Nursery and injury predicted by regression models.

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KEYWORDS: microevolution, freezing tolerance, cold hardiness, model verification

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